

DESCENDING AND TONOTOPIC PROJECTION PATTERNS FROM THE AUDITORY CORTEX TO THE INFERIOR COLLICULUS

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Abstract—The inferior colliculus (IC) receives many corticofugal projections, which can mediate plastic changes such as shifts in frequency tuning or excitability of IC neurons. While the densest projections are found in the IC's external cortices, fibers originating from the primary auditory cortex (AI) have been observed throughout the IC's central nucleus (ICC), and these projections have shown to be organized tonotopically. Some studies have also found projections from other core and non-core cortical regions, though the organization and function of these projections are less known. In guinea pig, there exists a non-core ventrorostral belt (VRB) region that has primary-like properties and has often been mistaken for AI, with the clearest differentiating characteristic being VRB's longer response latencies. To better understand the auditory corticofugal descending system beyond AI, we investigated if there are projections from VRB to the ICC and if they exhibit a different projection pattern than those from AI. In this study, we performed experiments in ketamine-anesthetized guinea pigs, in which we positioned 32-site electrode arrays within AI, VRB, and ICC. We identified the monosynaptic connections between AI-to-ICC and VRB-to-ICC using an antidromic stimulation method, and we analyzed their locations across the midbrain using three-dimensional histological techniques. Compared to the corticocollicular projections to the ICC from AI, there were fewer projections to the ICC from VRB, and these projections had a weaker tonotopic organization. The majority of VRB projections were observed in the caudal–medial versus the rostral–lateral region along an isofrequency lamina of the ICC, which is in contrast to the AI projections that were scattered throughout an ICC lamina. These findings suggest that the VRB

directly modulates sound information within the ascending lemniscal pathway with a different or complementary role compared to the modulatory effects of AI, which may have implications for treating hearing disorders. © 2015 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: corticofugal, feedback, auditory cortex, inferior colliculus, tonotopy, modulation.

INTRODUCTION

Traditionally, anatomical tracer studies have found that corticocollicular fibers from core and belt cortices primarily terminate in the nonlemniscal external cortices of the IC rather than the lemniscal ICC (Faye-Lund, 1985; Huffman and Henson, 1990; Herbert et al., 1991; Winer et al., 1998). However, there has been growing anatomical evidence that ICC receives direct, tonotopically-organized projections from core auditory areas including the primary auditory cortex, AI (Andersen et al., 1980; Feliciano and Potashner, 1995; Saldana et al., 1996; Budinger et al., 2000; Bajo and Moore, 2005; Coomes et al., 2005; Bajo et al., 2007; Lim and Anderson, 2007a; Malmierca and Ryugo, 2011). Studies in rat (Saldana et al., 1996), cat (Andersen et al., 1980), and ferret (Bajo et al., 2007) show that these projections are bilateral, though studies in gerbil (Budinger et al., 2000; Bajo and Moore, 2005) and in guinea pig (Coomes et al., 2005) found that the majority of these projections are ipsilateral. These corticofugal projections may influence plastic changes within the ICC, since there have been numerous studies showing that frequency tuning of ICC neurons can be finely shifted toward those of electrically stimulated AI neurons (Yan and Suga, 1998; Yan et al., 2005; Xiong et al., 2009). A more recent study also showed that electrical stimulation of AI neurons could cause extensive suppression of excitability of neurons in the ICC when paired with broadband noise stimulation (Markovitz et al., 2013). Less is known about corticofugal fibers that originate from non-AI cortical regions and target the ICC. In general, most studies have shown that only primary or core cortical regions project to the ICC (Winer et al., 1998; Bajo and Moore, 2005; Winer, 2005; Bajo et al., 2007), though one study found that the ICC also receives projections from non-core fields (Budinger et al., 2000). It is unknown whether these corticofugal projections from non-core regions are also tonotopically or topographically organized to the ICC and if

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Abbreviations: Δ BF, difference in the best frequencies between two sites; AC, auditory cortex; AI, primary auditory cortex; BF, best frequency; CSD, current source density; CYO, cytochrome oxidase; DC, dorsocaudal area; FRM, frequency response map; FSL, first-spike latency; IC, inferior colliculus; ICC, central nucleus of the inferior colliculus; PSTH, post-stimulus time histogram; VAF, ventral auditory field; VRB, ventrorostral belt.

they serve a different descending functional role compared to A1. Understanding the varying roles of the descending pathways from different cortical regions will improve our understanding of how the brain modulates ascending coding of auditory information for perception and learning. Clinically, it could also open up new targets and improve neural stimulation devices for treating hearing disorders, considering that patients are currently being implanted with electrode arrays that stimulate non-core or secondary auditory cortical regions for treating tinnitus (Friedland et al., 2007; De Ridder et al., 2011; Vanneste and De Ridder, 2012; Zhang, 2013; Engelhardt et al., 2014) but with very little understanding of the modulatory effects on the auditory system.

In the guinea pig, there is a non-core area called the ventrorostral belt, (VRB) (Wallace et al., 2000) that exhibits primary-like coding properties and was not differentiated from AI in early studies (Redies et al., 1989a,b). Located ventral and lateral to AI, neurons in VRB respond to frequency tones with low thresholds and are organized in a tonotopic pattern parallel to that of AI, thus causing the tonotopy to appear as a continuum of AI (Wallace et al., 2000). Originally distinguished from AI because of its long latencies and poor responses to noise (Wallace et al., 1999), VRB has also been shown to have the most units of all cortical fields that can discriminate conspecific vocalizations using a rate code (Grimsley et al., 2012). In terms of histological labeling, there are no clear transitions between AI and VRB for either myelin or cytochrome oxidase (CYO) staining (Wallace et al., 2000). VRB has moderate staining of myelin, less than the dense labeling in AI but similar to another core region called the dorsocaudal area (DC) (Wallace et al., 2000). In addition, VRB has dense labeling of CYO similar to that of AI and greater than the moderate labeling in DC. A previous study found that VRB does project to the inferior colliculus (IC) (Schofield, 2009), but it is unknown whether the VRB has direct projections to the ICC, or how they compare to those from AI.

In this study, we investigated the monosynaptic projection pattern from VRB to ICC and compared it to the pattern from AI to ICC within the anesthetized guinea pig. Because the small size of the VRB limits the ability to use tracer techniques for characterizing the precise spatial and functional organization of its corticofugal projections to the ICC, we used a previously developed antidromic stimulation technique (Lim and Anderson, 2007a), which allowed us to map descending projections between and characterize the physiological features of cortical and collicular neurons in the same animal. We found that both AI and VRB project to the ICC in a tonotopic manner, though with distinct differences in their projection pattern across and along the ICC laminae. These results suggest that AI and VRB have varying roles in processing both ascending and descending sound information within the lemniscal pathway.

EXPERIMENTAL PROCEDURES

Overview

Basic surgical procedures and methods for neural recording and stimulation were similar to those

presented in previous work (Lim and Anderson, 2006, 2007a; Straka et al., 2013). Ketamine-anesthetized guinea pigs were used in accordance with policies of the University of Minnesota's Institutional Animal Care and Use Committee. Silicon-substrate, 32-site Michigan electrode arrays (NeuroNexus Technologies, Ann Arbor, MI, USA) were used to electrically stimulate the ICC and record the corresponding neural responses within the auditory cortex (AC). Appropriate placement of the array sites within the ICC and AC was guided by acoustic-driven responses (Wallace et al., 2000; Snyder et al., 2004; Lim and Anderson, 2007b). Array sites in the ICC were individually stimulated and multi-unit spiking responses were recorded in AI and VRB. When antidromic activity was detected in AI or VRB, the minimal stimulation threshold and location across the ICC was found and analyzed to determine if there is a spatial distribution across the ICC lamina for corticofugal projections.

Surgery

Experiments were performed on 23 Hartley guinea pigs (380 ± 53 g, Elm Hill Breeding Labs, Chelmsford, MA, USA). Animals were initially anesthetized with an intramuscular injection of ketamine (40 mg/kg) and xylazine (10 mg/kg), and were given periodic supplements to maintain an areflexic state. After fixing the animal into a stereotaxic frame (David Kopf Instruments, Tujunga, CA, USA), the right side of the cortex was exposed from the caudal end of the occipital lobe to the middle cerebral artery of the temporal lobe. The dura was removed, micromanipulators were used to insert the arrays into the ICC and AC, and the exposed brain was covered with agarose gel.

Stimulation and recording setup

All experiments were performed in an acoustically- and electrically-shielded chamber and controlled by a computer interfaced with TDT System 3 hardware (Tucker-Davis Technology, Alachua, FL, USA) using custom software written in MATLAB (MathWorks, Natick, MA, USA). For acoustic stimulation, sound was presented via a speaker coupled to the left ear through a hollow ear bar. The speaker-ear bar system was calibrated using a 0.25-in. condenser microphone (ACO Pacific, Belmont, CA, USA) connected to the ear bar via a short plastic tube representing the ear canal.

All neural signals were passed through analog DC-blocking and anti-aliasing filters from 1.6 Hz to 7.5 kHz. The sampling frequency used for acoustic stimulation was 195 kHz and for neural recording was 24 kHz. Electrical stimulation up to 64 μ A was presented on different sites on the ICC array in a monopolar configuration with a ground return in the neck muscles. The pulses were biphasic, charge-balanced, cathodic-leading, and 205- μ s/phase. The recording ground needle was positioned either under the skin approximately 2 cm rostral to bregma or directly in the brain in the parietal lobe. No obvious differences in results were observed when using the different recording grounds.

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